

MYCOTAXON

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***Entoloma* species from New South Wales and northeastern Queensland, Australia**DAVID L. LARGENT^{1*}, SARAH E. BERGEMANN², & SANDRA E. ABELL-DAVIS³¹*Biological Sciences, Humboldt State University, 1 Harpst St, Arcata CA 95521, USA*²*Evolution and Ecology Group, Biology Department, Middle Tennessee State University,
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ABSTRACT — Seven new species in the *Prunuloides* clade of the *Entolomataceae* are described here: *Entoloma hymenidermum* is diagnosed by blackish blue basidiomata, isodiametric basidiospores and moderately broad pileocystidia; *E. violaceotinctum* has a violet-tinged pileus, violaceous-tinged stipe, and broad inflated pileocystidia; *E. discoloratum* possesses a subviscid yellow-tinged white pileus; *E. kewarra* is distinguished by its yellow pileus and stipe, both with a white and then eventually greenish yellow context; *E. pamela* has a smooth, bright yellow, dry pileus; *E. rugosiviscosum* has a yellow-brown, rugose viscid pileus; and *E. guttulatatum* is distinguished by lamellae with droplets that become reddish brown on drying.

KEY WORDS — *Basidiomycota*, phylogeny, taxonomy

Introduction

A morphologically based classification has given rise to two interpretations of the genus *Entoloma* (*Agaricales*, *Entolomataceae*). In one approach, taxa are placed into a single genus and the subgenera are defined mostly by the pileus surface, the pileipellis structure, and the basidiospore size, shape, and angularity (Noordeloos 1992, 2005; Co-David et al. 2009; Noordeloos & Gates 2012). In a second approach, *Entoloma* is accepted in a restricted sense with additional genera recognized based on biochemical features, pigmentation, location of clamp connections, and stature types in addition to the pileus surface, the pileipellis structure, and the basidiospore size, shape, and angularity (Orton 1991, Largent 1994, Baroni & Matheny 2011, Baroni et al. 2011). Recent comprehensive phylogenetic analyses of the *Entolomataceae* have highlighted

many issues inherent with the morphologically based classifications by showing that many of the segregate genera or infrageneric groups are not monophyletic (Co-David et al. 2009; Baroni & Matheny 2011), suggesting the need to re-evaluate key characters used for delineation of segregate genera.

The majority of species of *Entoloma* s.s. are supported in one of two clades, either the Rhodopolioid or Prunuloides clade (Co-David et al. 2009, Baroni & Matheny 2011). The species described in this paper share similar features with many members of the Prunuloides clade: a tricholomatoid or naucorioid stature (Largent 1986), isodiametric basidiospores, rather short and broad hyphae in the pileus trama, and abundant clamp connections in the pileipellis.

The Prunuloides clade also accommodates segregate genera. *Entocybe* T.J. Baroni et al. was erected for species with finely pustulate basidiospores with bumps and 6–10 facets when viewed in polar view (Baroni et al. 2011). *Calliderma* (Romagn.) Largent was erected for species with a tricholomatoid stature, a pruinose, tomentose, velutinous, or rivulose pileus corresponding to a hymeniform pileipellis, and septate hyphae with or without clamp connections.

Australian field investigations from 2009–2012 within northeastern Queensland's Wet Tropics Bioregion and from 2010–2012 in the temperate rainforests of central New South Wales have uncovered several novel entolomataceous species (Largent & Abell-Davis 2011; Largent et al. 2011a,b, 2013a,b; Bergemann et al. 2013). Here, we describe seven new species representing *Entoloma* s.s.: *E. discoloratum*, *E. guttulatum*, *E. hymenidermum*, *E. kewarra*, *E. pamela*, *E. rugosiviscosum*, and *E. violaceotinctum*.

Materials & methods

Macromorphological and micromorphological features

Techniques and equipment for collecting and describing basidiomata in the field, GPS coordinates, microscopy of dried collections including how basidiospores were measured, and digital microphotographs have been described in Largent et al. (2011a, b), while techniques for color descriptions using Kornerup & Wanscher (1978) and factors determined from mathematical analyses in the descriptions are covered in Largent et al. (2013a,b). All collections for New South Wales cited in the 'Additional collections examined' were deposited in The Plant Pathology Herbarium, Orange Agricultural Institute (DAR). Collections made in Queensland were deposited in the Australian Tropical Herbarium (CNS). All holotype and isotype collections are deposited in the herbaria designated using acronyms from Thiers (2012).

DNA sequences and phylogenetic analyses

Thirty-four sequences from three partial genes including the mitochondrial small subunit ribosomal RNA (mtSSU), the nuclear large subunit ribosomal RNA (LSU), and second largest subunit of RNA polymerase II (RPB2) were generated for this phylogenetic analysis along with sequences obtained from GenBank (TABLE 1). The extraction and Polymerase Chain Reaction (PCR) protocols for the mtSSU, LSU and the RPB2 follow

TABLE 1. Collections used in the phylogenetic analyses. New sequences generated for this study are shown in bold. Square bracketed annotations indicate species names applied in GenBank that differ from those in the phylogram (FIG. 1).

SPECIES FROM GENBANK	COLLECTION IDENTIFIER	GENBANK ACCESSION NUMBERS		
		mtSSU	LSU	RPB2
<i>Entocybe haastii</i>	DLL9868	JQ793644	JQ793651	JQ793658
	DLL10087	JQ793645	JQ793652	JQ793659
<i>Ec. nitida</i> [<i>E. nitidum</i>]	7526 TJB	GU384602	GU384626	GU384655
<i>Ec. nitida</i> [<i>E. alcedicolor</i>]	210	GQ289292	GQ289152	GQ289224
<i>Ec. trachyospora</i> [<i>R. trachyospora</i>]	5856 TJB	GU384605	GU384629	GU384658
<i>Ec. turbida</i> [<i>E. turbidum</i>]	27	GQ289341	GQ289201	GQ289269
	6949 TJB	GQ289341	GQ289201	GQ289269
<i>Ec. vinacea</i> [<i>E. vinaceum</i>]	8870 TJB	GU384598	GU384631	GU384651
<i>Clitopilus</i> aff. <i>hobsonii</i>	DLL9586	KJ021688	KJ021698	KC816912
<i>Entoloma albomagnum</i>	427	KC710165	KC710137	—
<i>E. bloxamii</i>	219	GQ289294	GQ289154	GQ289226
<i>E. aff. bloxamii</i>	628	KC710189	KC710159	—
	Thiers 53901	KC710168	KC710139	—
<i>E. aff. whiteae</i> [<i>E. prunuloides</i>]	4765 TJB	—	AY700180	DQ385883
<i>Entoloma</i> sp. [<i>E. haastii</i>]	BY21	—	AF261309	—
<i>Entoloma</i> sp.	292, 9895 TJB	GQ289296	GQ289156	GQ289228
<i>E. caccabus</i>	17	GQ289295	GQ289155	GQ289227
<i>E. caesiolamellatum</i> [<i>E. bloxamii</i>]	6117 TJB	—	AF261289	—
<i>E. callidermum</i>	609	KC710183	KC710153	—
<i>E. calongei</i>	322	GQ289298	GQ289158	—
<i>E. clypeatum</i>	41	KC710164	KC710136	—
<i>E. coeruleogracilis</i> [<i>E. haastii</i>]	216	GQ289308	GQ289168	GQ289239
	217	GQ289309	GQ289169	GQ289240
<i>E. coeruleoviride</i>	609	KC710162	KC710134	KC710057
<i>E. cretaceum</i>	213	GQ289302	GQ289162	GQ289233
<i>E. discoloratum</i>	DLL10217	JQ793646	JQ793653	JQ793660
<i>E. ferruginans</i>	11CA032	KJ021689	KJ021699	KJ021693
<i>E. fibulatum</i> [<i>Calliderma fibulatum</i>]	SP393751	—	FJ973677	—
<i>E. flavifolium</i>	6215 TJB	GU384597	AF261301	GU384644
	621	KC710179	KC710150	—
<i>E. fragilum</i>	MCA2415	KJ021690	KJ021700	KJ021694
<i>E. fumosobrunneum</i> [<i>Entoloma</i> sp.]	2005113	KC710185	KC710155	—
	2005120	KC710186	KC710156	—
<i>E. gelatinosum</i>	212	GQ289305	GQ289165	GQ289236
<i>E. griseolazulinum</i>	i11	GQ289306	GQ289166	GQ289237
<i>E. guttulatum</i>	DLL9791	—	—	JQ793656
<i>E. hymenidermum</i>	DLL10025	JQ793648	JQ793642	—
	DLL10054	—	JQ793649	—
<i>E. illinitum</i>	MCA2488	—	KJ021701	KJ021695
<i>E. indigoticoumbrinum</i>	83	GQ289318	GQ289178	GQ289249
<i>E. kermantii</i>	222	GQ289313	GQ289173	GQ289244
<i>E. kewarra</i>	DLL10055	—	JQ793655	JQ793662
<i>E. lividoalbum</i>	233	KC710182	KC710152	—

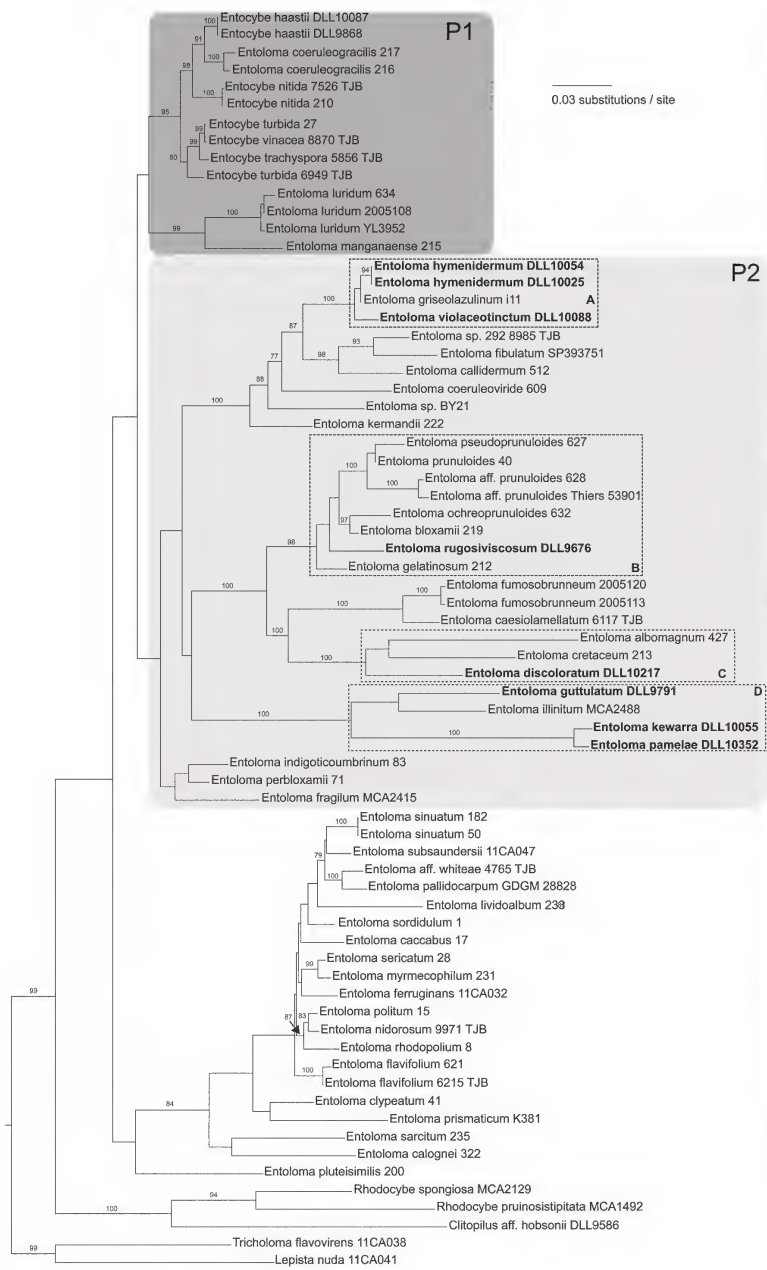
TABLE 1, concluded

SPECIES FROM GENBANK	COLLECTION IDENTIFIER	GENBANK ACCESSION NUMBERS		
		mtSSU	LSU	RPB2
<i>E. luridum</i>	2005108	KC710175	KC710146	KC710192
	634	KC710170	KC710141	—
	YL3952	KC710177	KC710148	—
<i>E. manganaense</i>	215	KC710172	KC710143	—
<i>E. myrmecophilum</i>	231	GQ289314	GQ289174	GQ289245
<i>E. nidorosum</i>	9971 TJB	GU384596	GU384617	GU384643
<i>E. ochreoprunuloides</i> [Entoloma sp.]	632	KC710176	KC710147	—
<i>E. pallidocarpum</i>	GDGM 28828	JQ993074	JQ410331	JQ993080
<i>E. pamelae</i>	DLL10352	—	KJ021702	KJ021696
<i>E. perbloxamii</i>	71	GQ289318	GQ289178	GQ289249
<i>E. pluteisimilis</i>	200	GQ289320	GQ289180	GQ289251
<i>E. politum</i>	15	GQ289321	GQ289181	GQ289252
<i>E. prismaticum</i>	K381	—	AB692006	AB692016
<i>E. prunuloides</i>	40	GQ289324	GQ289184	GQ289255
<i>E. pseudoprunuloides</i> [Entoloma sp.]	627	KC710169	KC710140	—
<i>E. rhodopolium</i>	8	GQ289327	GQ289187	GQ289258
<i>E. rugosiviscosum</i>	DLL9676	JQ793647	JQ793654	JQ793661
<i>E. sarcitum</i>	235	GQ289328	GQ289188	GQ289259
<i>E. sericatum</i>	28	GQ289329	GQ289189	—
<i>E. sinuatum</i>	50	GQ289333	GQ289193	GQ289264
	182	KC710184	KC710154	—
<i>E. sordidulum</i>	1	GQ289334	GQ289194	GQ289265
<i>E. subsaundersii</i>	11CA047	—	KJ021703	KJ021697
<i>E. violaceotinctum</i>	DLL10088	JQ793643	JQ793650	JQ793657
<i>Lepista nuda</i>	11CA041	KJ021692	KJ021705	KJ136110
<i>Rhodocybe pruinostipitata</i>	MCA1492	GU384608	GU384627	GU384653
<i>R. spongiosa</i>	MCA2129	GU384604	GU384628	GU384657
<i>Tricholoma flavovirens</i>	11CA038	KJ021691	KJ021704	KC816997

Largent et al. (2011b). The primer combinations rpb2-i6f and rpb2-i7r (Co-David et al. 2009), rpb2-EntF2 and rpb2-EntR4 (Largent et al. 2013b) and fRPB2-5F and bRPB2-7R (Liu et al. 1999; Matheny 2005) were also used. Sequences were generated on an Applied Biosystems 3130xl Genetic Analyzer at Middle Tennessee State University using the sequencing protocols outlined in Largent et al. 2011b.

Sequences were edited using Sequencher 4.2.2 (Gene Codes Corporation, Ann Arbor, MI) and an automated alignment performed using MAFFT v. 7 (Katoh & Standley 2013). Introns in the RPB2 and hypervariable regions and large introns in the mtSSU were excluded prior to analysis. The alignment lengths were 570 bp (mtSSU), 1506 bp (LSU), and 1165 bp (RPB2). A Maximum Likelihood analysis based on 100

FIGURE 1. Topology of the maximum-likelihood phylogram (mtSSU+LSU+RPB2) highlighting the subclades within the Prunuloides clade that included the new species proposed here (P1 and P2). Each sequence is labeled with the GenBank-listed isolate identifier and species placement for clusters (A–D) are described in the text. Branches with $\geq 70\%$ support from 1000 rapid bootstraps are shown. *Lepista nuda*, *Clitopilus* aff. *hobsonii*, *Rhodocybe pruinostipitata*, *R. spongiosa*, and *Tricholoma flavovirens*, served as outgroups, and the tree was rooted with *L. nuda*.



Prunuloides

Rhodopolioide

ML replicates and specifying a GTRGAMMA model in RAXML-HPC v. 7.2.8 ALPHA (Stamatakis 2006) was carried out with a partitioned dataset: RPB2 (across each codon position for three partitions), and separate partitions for the mtSSU and LSU. Support values were based on bootstrap proportions on 1000 bootstrap replicates (Stamatakis et al. 2008).

Results

The phylogenetic analysis based on combined mtSSU+LSU+RPB2 genes place all seven *Entoloma* species into the *Prunuloides* clade (FIG. 1). Clade P1 contains a cluster of species recognized as *Entocybe* (BS = 98) and a sister clade including *E. luridum* Hesler and *E. manganaense* G.M. Gates & Noordel. (BS = 99), a relationship that remains unsupported here. Clade P2 contains all the Australian species described in this report: 1) *Entoloma hymenidermum* and *E. violaceotinctum* cluster with several *Calliderma* species and share a close affinity with *E. griseolazulinum* Manim. & Noordel. (BS = 100, FIG. 1, A); 2) *Entoloma rugosiviscosum* clusters with *E. bloxamii* (Berk. & Broome) Sacc., *E. gelatinosum* E. Horak, and species within the *E. prunuloides* species complex (BS = 98, FIG. 1, B), whereas *E. discoloratum* cluster with *E. cretaceum* G.M. Gates & Noordel. and *E. albomagnum* G.M. Gates & Noordel. (BS = 100, FIG. 1, C); and 3) *E. guttulatatum*, *E. pamela* and *E. kewarra* cluster together with *E. illinitum* Largent & Aime (BS = 100, FIG. 1, D).

Taxonomy

Entoloma hymenidermum Largent, sp. nov.

PLATES 1–2

MYCOBANK MB804379

Differs from *Entoloma griseolazulinum* by the broader stipe, smaller basidia, and shorter basidiospores.

TYPE — Australia, Queensland, Cook Region, Yorkeys Knob coastal vine forest, within 20m of 16°49'00.3"S 145°43'49.3"E, 20 March 2011, DL Largent 10054 (holotype BRI; isotype CNS).

ETYMOLOGY — named for the hymeniderm pileipellis.

PILEUS 29–70 mm broad, 6.5–15.0 mm high; opaque, not hygrophanous, not translucent-striate; at first convex to broadly convex, sometimes campanulate-convex, upon expansion and maturity becoming plane and finally uplifted and undulate, sometimes broadly umbonate; entirely minutely velvety to suede-like but forming irregularly radial cracks near the margin when mature, always dull; when young blackish blue with the bluish color dominant (20F8) in the center, slightly lighter (20F6) elsewhere, on drying dark blue (20E-F6), when old blackish blue with the black color dominating (19F4); margin incurved at first, then decurved, finally plane then uplifted, entire then eroded; context 1–3 mm thick above the stipe, bluish. ODOR mild, at times somewhat fragrant.



PLATE 1. *Entoloma hymenidermum* (DLL10054 holotype). A. Basidiomata. B. Stipe surface. C. Pileus surface. Bar scale: A = 15 mm; B = 5 mm; C = 8 mm.

TASTE mild to at times somewhat bitter. LAMELLAE 11–29 mm long, 2.7–10.5 mm deep, narrow to moderately broad and eventually nearly broad; uncinately sinuate with a decurrent tooth; close then subdistant; white to between white and orange white (5A1–2) when young becoming greyish orange (5A-B4–5) or (5A3–4) with basidiospore maturation; margin smooth and concolorous. STIPE 27–79 mm long, 4–10.5 mm broad at the apex, 4–14.5 mm broad at base, equal to clavate; longitudinally appressed fibrillose from the apex to the basal tomentum, markedly striate, and sometimes twisted; fibrils various

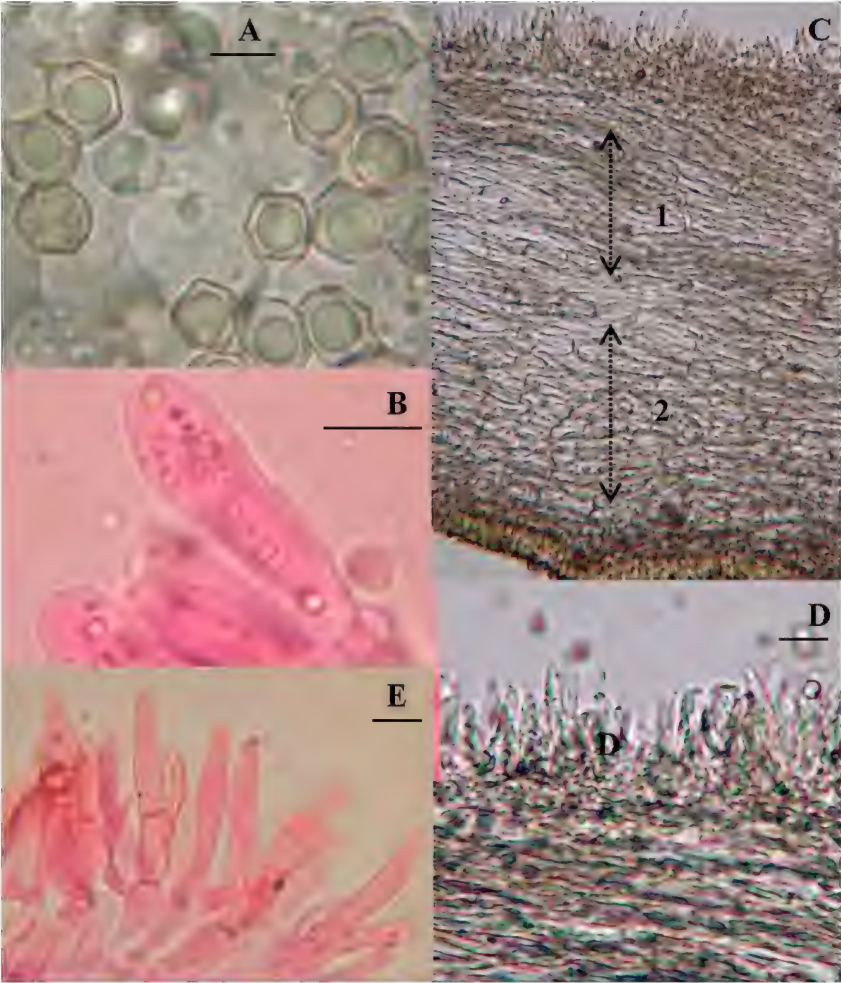


PLATE 2. *Entoloma hymenidermum* (DLL10054 holotype). A. Basidiospores. B. Basidium, basidioles. C. Pileipellis radial section at pileus disc; pileal trama cylindric hyphae (top arrows), broad hyphae (bottom arrows). D. Pileipellis (calliderm and outer pileal trama). E. Pileipellis, a calliderm (section slightly squashed). Bars: A = 8 μ m; B = 12 μ m; C₁ = 190 μ m; C₂ = 230 μ m; D = 5 μ m; E = 10 μ m.

shades of blackish blue, more bluish (20F6) when young, fading slightly (20E4) when drying, and more blackish or dark bluish grey (19E-F3 or 4) when old, background color white, base of the stipe white; context stuffed at first, quickly becoming hollow with maturity; basal tomentum scarce, white. BRUISING REACTIONS none.

BASIDIOSPORES distinctly 5–6-angular, others are typically collapsed when mounted in 3% KOH, in profile and dorsiventral views isodiametric to subisodiametric, rarely heterodiametric, isodiametric in polar view, $6.8\text{--}10.0$ (-10.4) $\times$ (5.9) $6.2\text{--}8.8$ (-9.0) μm ($x = 8.3 \pm 0.6 \times 7.4 \pm 0.6$ μm ; $E = 1.00\text{--}1.31$; $Q = 1.12 \pm 0.07$ (isodiametric); $n = 125/4$). BASIDIA narrowly clavate and tapered, relatively long and narrow, $38.9\text{--}48.9 \times 9.7\text{--}14.5$ μm ($x = 42.8 \pm 3.1 \times 11.4 \pm 1.32$ μm ; $E = 3.25\text{--}4.00$; $Q = 3.78 \pm 0.33$; $n = 16/2$); 4-sterigmate. SCLEROBASIDIA absent. HYMENIAL CYSTIDA absent. LAMELLAR EDGE fertile. CHEILOCYSTIDIA and PLEUROCISTIDIA absent. LAMELLAR TRAMAL HYPHAE subparallel, in the center to near the subhymenium, mostly relatively long and broad and inflated with rounded end walls, $41.0\text{--}170 \times 8.5\text{--}42.1$ μm , rarely long and narrow, not inflated and then 170×4 μm . PILEIPELLIS $28.6\text{--}89.7$ μm in depth, composed of a chain of 3–5 entangled cells, the basal portion developing from the outer layer of the pileal trama and the terminal cells erect, distinct, forming a palisade of pileocystidia that are not tightly packed. PILEOCYSTIDIA versiform (cylindric, narrowly cylindro-clavate, clavate, obclavate, to ventricose-rostrate with the rostrum up to 2 μm long), $22.4\text{--}58.6 \times 4.4\text{--}18.6$ (-21.3) μm ($x = 41.6 \pm 10.5 \times 10.6 \pm 4.5$ μm ; $E = 1.20\text{--}6.3$ (rarely $8.8\text{--}9.8$); $Q = 4.60 \pm 2.17$; $n = 20/2$). PILEAL TRAMA composed of 2 layers, a layer adjacent to the subhymenium, $228\text{--}312$ μm in depth composed of inflated, relatively short and broad hyphae, $34.4\text{--}137.6 \times 9.4\text{--}24.2$ μm ($n = 11/1$), and a narrow layer, $119\text{--}163$ μm deep, composed of cylindric entangled hyphae, $30\text{--}110 \times 3\text{--}6$ μm , the outer most portion forming the pileipellis. STIPTIPELLIS a cutis. CAULOCYSTIDIA and HYMENIAL CLUSTERS absent. OLEIFEROUS HYPHAE present in the subhymenium. BRILLIANT GRANULES and LIPOID GLOBULES absent. PIGMENTATION cytoplasmic in the pileipellis, in 3% KOH at first bluish brown and then colorless due to its solubility in the medium. CLAMP CONNECTIONS present in all tissues, small and inconspicuous, easily observed in the branched portion of the pileal tramal hyphae just beneath the pileipellis.

ECOLOGY & DISTRIBUTION — At times abundant, scattered, or solitary in sandy humus with leaf litter, in coastal vine forest near *Maytenus fasciculiflora* Jessup, *Canarium australianum* F. Muell. var. *australianum*, *Polyalthia nitidissima* Benth., and *Guioa acutifolia* Radlk., often adjacent to *Drynaria sparsisora* (Desv.) T. Moore, and at times sheltered by decaying logs and at other times near the mangrove zone, Clifton Beach to Yorkeys Knob Beach, northern Queensland, early to late March.

ADDITIONAL COLLECTIONS EXAMINED — AUSTRALIA. QUEENSLAND, Cook Region, Clifton Beach, $16^{\circ}48'50.6''\text{S}$ $145^{\circ}43'46.6''\text{E}$, 9 March 2010, PN 016, PN 017; Yorkeys Knob, $16^{\circ}45'45.7''\text{S}$ $145^{\circ}40'29.6''\text{E}$, 29 January 2011, PN 51 3 February 2011, PN 56; $16^{\circ}48'33''\text{S}$ $145^{\circ}40'32''\text{E}$, 8 March 2010, PN 012; 10 March 2010, PN 012A; $16^{\circ}45'43.8''\text{S}$ $145^{\circ}40'27.5''\text{E}$, 14 March 2011, DL Largent 10025.

DISTINCTIVE CHARACTERS — Tricholomatoid basidiomata, minutely velvety bluish black pileus, longitudinally appressed fibrillose dark bluish grey stipe, 2-layered pileal trama, and basidiospores averaging $8 \times 7 \mu\text{m}$.

COMMENTS — In the phylogeny, *E. hymenidermum* and *E. violaceotinctum* cluster with species that have bluish basidiomata with a finely to distinctly velutinous or tomentose pileus surface, a hymeniform-type (calliderm or erect trichoderm) pileipellis, strongly and distinctly angular basidiospores, and an outer pileus trama of cylindric cells, at least on the disc. Species with a hymeniform type pileipellis are often recognized in *Calliderma* (Aime et al. 2010; Karstedt & Capelari 2010). However, *E. kermantii* G.M. Gates & Noordel., which also falls in this clade, possesses a cutis, a feature inconsistent with the generic circumscription of *Calliderma*. Furthermore, *C. pruinatocutis* (E. Horak) Karstedt & Capelari and *C. rimosum* Karstedt & Capelari (Karstedt et al. 2010) are placed in a distant and unrelated clade (Baroni & Matheny 2011). Without support for the monophyly of *Calliderma*, we classify the species described here as *Entoloma*.

Entoloma hymenidermum is morphologically similar to several species that have a tricholomatoid habit, dark bluish or bluish-black tinged pileus, fibrillose stipe, 5–6 angled basidiospores, clavate to versiform pileocystidia, clamp connections on the pileipellis hyphae, and lack of cheilocystidia.

Entoloma violaceotinctum from New South Wales differs from *E. hymenidermum* in its larger basidiomata with violaceous tones, a stipe that discolors purplish and then brownish when handled, basidiospores averaging $9 \times 8 \mu\text{m}$, longer (47–73 μm) basidia, and occurrence in deep leaf humus and organically rich soils in a northern warm temperate rain forest. *Entoloma griseolazulinum*, described from Kerala State (India), has a more slender (3–5 mm wide) stipe, longer (10–13 μm) basidiospores, and larger (47–71 $\times$ 11–16 μm) basidia (Manimohan et al. 2006). *Calliderma indigoferum* (Ellis) Largent, collected in a swamp among mosses in New Jersey, has an indigo blue (18F3) pileus (75–100 mm broad), white $\pm$ blue-tinged blue stipe, and large clamp connections (Largent 1994). *Calliderma caeruleosplendens* Largent et al. (Pakaraima Mountains, Guyana) is distinguished by its densely matted tomentose dark blue pileus, very dark blue stipe, and its broadly clavate, napiform, or broadly obclavate pileocystidia (Aime et al. 2010). *Entoloma rugosopruinatum* Corner & E. Horak, reported from Sabah (Malaysia) and Kerala State (India), differs from all of these species primarily by the clampless hyphae (Horak 1980; Manimohan et al. 1995, 2006).

Entoloma callidermum (Romagn.) Noordel. & Co-David from Africa and Malaysia can be differentiated from *E. hymenidermum* by the violet and/or

bister tinges in the pileus and the stipe, 5–7-angled basidiospores, smaller basidia ($27\text{--}35 \times 6\text{--}11 \mu\text{m}$), and the absence of a 2-layered lamellar tramal hyphae (Romagnesi 1956, as *Rhodophyllus callidermus*; Morgado et al. 2013). However, the original description provided by Romagnesi (1956) may include segregate species (Eyssartier et al. 2012).

Calliderma fibulatum Karstedt & Capelari, *Entoloma simillimum* Corner & E. Horak, *E. marinum* Corner & E. Horak, *E. ducale* E. Horak, *E. divum* Corner & E. Horak, and *E. burkilliae* Massee resemble *E. hymenidermum* and *E. violaceotinctum* in basidiome color and the pileipellis but differ in their 5–11 μm broad fusoid to cylindric pileocystidia and the presence of cheilocystidia (Horak 1980, Karstedt & Capelari 2010). *Entoloma coeruleomagnum* G.M. Gates & Noordel. differs by its palisadoderm pileipellis and *E. kermantii* by its cutis (Noordeloos & Gates 2012).

***Entoloma violaceotinctum* Largent, sp. nov.**

PLATES 3-4

MYCOBANK MB804380

Differs from *Entoloma hymenidermum* by its pileus and stipe with violet or violaceous tones, stipe that bruises when handled, larger basidiospores, and longer basidia.

TYPE — Australia, New South Wales, Strickland State Forest, lower track, central Hunter District, within 20m of $33^{\circ}22'49''\text{S}$ $151^{\circ}19'32''\text{E}$, 14 April 2011, DL Largent 10088 (holotype DAR).

ETYMOLOGY — Derived from the Latin *violaceus* (= violet) + *tinctus* (= tint) for the violet tinted pileus and stipe.

PILEUS 40–100 mm broad, 7–40 mm high; opaque and even, hygrophanous, not translucent-striate; broadly umbonate at all times, convex to broadly convex at first, then plane to uplifted with age; velvety, at times appearing stippled with minute, pointy hairs; dark violet to blackish blue (18F4–5 or 19F5–6) fading to dull violet to dark blue (18–19E4–5) with a darker center (dark violet grey 17F2), dull; margin incurved then decurved, entire; context cream-colored except for the pellicle that is concolorous with the surface, 6–10 mm broad above the stipe, 1–3 mm broad at the margin. ODOR mild and fragrant in young specimens, strong but undefined in older specimens. TASTE indistinct in younger specimens, unpleasant in older specimens. LAMELLAE 15–45 mm long, 6–15 mm deep, moderately broad; adnexed and close then sinuate and subdistant, seceding with age; at first white or off-white to pale orange (5A3 or 15A2–3) then light orange (5A4) with basidiospore maturation; margin smooth and concolorous. STIPE 40–92 mm long, 6–16 mm broad at apex, 5–13 mm broad at base, at times flattened and then $17 \times 7 \text{ mm}$ at the apex and $13 \times 10 \text{ mm}$ at the very base, versiform in shape (equal, subclavate, clavate or broad at apex and more narrow at base); appressed fibrillose; fibrils medium



PLATE 3. *Entoloma violaceotinctum* (DLL10088 holotype). A. Basidiomata. B. Stipe surface. C. Pileus surface. Bar: A = 20 mm; Bar scale: B. = 16 mm; C = 35 mm.

violet grey (18D2–3), base color yellowish white to light orange (4A2 or 5B3); context white, at first stuffed with maturity becoming hollow and then snaps easily; basal tomentum absent. BRUISING REACTIONS on the stipe occurs after handling, becoming purplish (18E4) and then brownish (5E4).

BASIDIOSPORES 5–6-angled, angles typically distinct, often with irregularly wavy walls in dried specimens, isodiametric to subisodiametric in profile and dorsiventral views, isodiametric in polar view, $7.8\text{--}10.2 \times 7.1\text{--}9.2 \mu\text{m}$ ($x = 8.9$

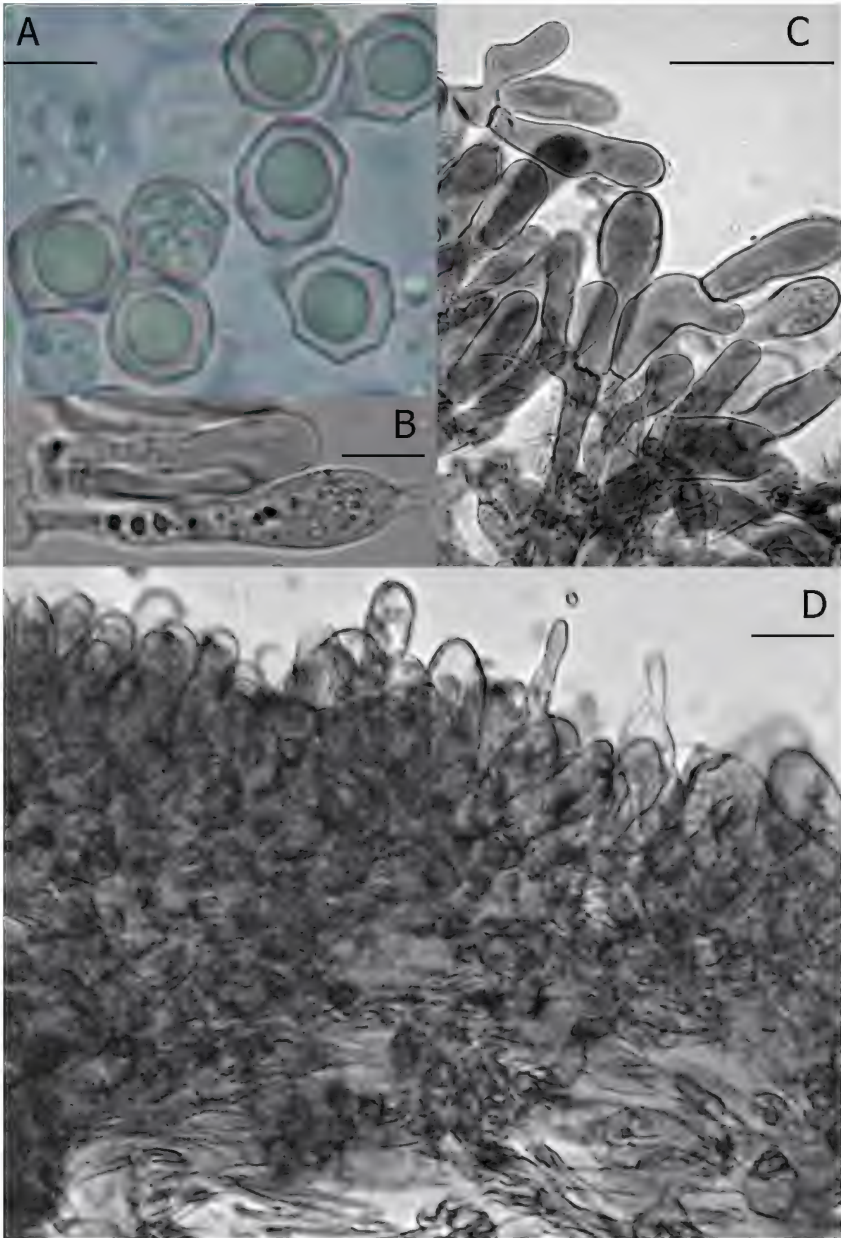


PLATE 4. *Entoloma violaceotinctum* (DLL10088 holotype). A. Basidiospores. B. Basidia, basidioles. C. Pileipellis branching pattern. D. Pileipellis (calliderm and outer pileal trama). Bars: A = 8 μ m; B = 13 μ m; C, D = 30 μ m.

$\pm 0.7 \times 8.0 \pm 0.7 \mu\text{m}$; $E = 1.00\text{--}1.24$; $Q = 1.11 \pm 0.06$ (isodiametric); $n = 56/2$). BASIDIA clavate, very long and relatively narrow, often tapered to $2\text{--}3 \mu\text{m}$, usually with rather large droplets or globules in mature forms, 4-sterigmate, $47.1\text{--}73.1 \times 10.8\text{--}14.2 \mu\text{m}$ ($\bar{x} = 57.4 \pm 7.8 \times 12.6 \pm 0.9 \mu\text{m}$; $E = 3.63\text{--}5.77$; $Q = 4.57 \pm 0.58$; $n = 25/2$). SCLEROBASIDIA absent. HYMENIAL CYSTIDIA absent. LAMELLAE in section composed of two layers, a hymenium $31\text{--}45 \mu\text{m}$ thick, subhymenium $13\text{--}22 \mu\text{m}$ thick with two lateral strata, each $17\text{--}30 \mu\text{m}$ thick, and a central layer ($86\text{--}95 \mu\text{m}$ wide). LAMELLAR TRAMA HYPHAE subparallel, relatively short, consisting of two types, slender, narrow hyphae, $61.2\text{--}113.1 \times 3.3\text{--}8.0 \mu\text{m}$ ($n = 9/2$) forming between the subhymenium and the center of the lamellae and inflated hyphae, $39.5\text{--}105.3 \times 9.5\text{--}22.2 \mu\text{m}$ ($n = 22/2$) found in the center. PILEIPELLIS $36\text{--}54 \mu\text{m}$ in depth, a hymeniderm of pileocystidia, composed of entangled layer of hyphae, typically 3 cells long, with the pileocystidia as 1–3 terminal cells branching from a subterminal cell. PILEOCYSTIDIA the terminal cells of branched hyphae that originate from the outer pileal trama, clavate to broadly obclavate, $29.8\text{--}82.7 \times 8.2\text{--}39.3 \mu\text{m}$ ($\bar{x} = 48.9 \pm 12.3 \times 14.9 \pm 4.5 \mu\text{m}$; $E = 1.01\text{--}6.36$; $Q = 3.55 \pm 1.14$; $n = 38/2$). PILEAL TRAMA composed of two layers, an entangled layer ($61\text{--}210 \mu\text{m}$ thick) with slender hyphae, $68.6\text{--}112.6 \times 3.7\text{--}9.1 \mu\text{m}$; ($n = 7/1$) the outer portion of which produce the pileipellis and an adjacent layer ($475\text{--}539 \mu\text{m}$ thick) composed mostly of inflated hyphae, $50\text{--}237 \times 12.5\text{--}26.0 \mu\text{m}$ ($n = 15/2$). STIPITPELLIS a cutis. CAULOCYSTIDIA and HYMENIAL CLUSTERS absent. OLEIFEROUS HYPHAE present in the trama of the lamellae and the pileus. BRILLIANT HYPHAE and LIPOID GLOBULES absent. PIGMENTATION cytoplasmic in the pileipellis, in 3% KOH at first bluish brown and then colorless due to its solubility in the medium. CLAMP CONNECTIONS rather large and present in all tissues.

ECOLOGY & DISTRIBUTION — Typically gregarious in mid-April, then scattered in early May, in deep leaf humus and organic rich soil, near *Syncarpia glomulifera* (Sm.) Nied., *Ceratopetalum apetalum* D. Don, and *Doryphora sassafras* Endl.), and *Schizomeria ovata* D. Don hosts, New South Wales, central Hunter District, Strickland State Forest, mid April through early May.

ADDITIONAL COLLECTIONS EXAMINED — AUSTRALIA. NEW SOUTH WALES, central Hunter District, Strickland State Forest, lower car park area, 19 April 2011, DL Largent 10128; $33^{\circ}22'47''\text{S}$ $151^{\circ}19'28''\text{E}$, DL Largent 10129; $33^{\circ}22'47''\text{S}$ $151^{\circ}19'27''\text{E}$, 28 April 2011, DL Largent 10168; $33^{\circ}22'47''\text{S}$ $151^{\circ}19'28''\text{E}$; 8 May 2011, DL Largent 10215; $33^{\circ}22'48''\text{S}$ $151^{\circ}19'30''\text{E}$, *Banksia* loop path, 19 April 2011; $33^{\circ}22'19''\text{S}$, $151^{\circ}19'11''\text{E}$, 3 May 2011, DL Largent 10183.

DISTINCTIVE CHARACTERS — Tricholomatoid basidiomata with violaceous tones, a stipe that discolours purplish then brownish when handled, basidiospores averaging $9 \times 8 \mu\text{m}$, long ($47\text{--}73 \mu\text{m}$) basidia, and its occurrence in deep leaf humus.

COMMENTS — Refer to the Comments section under *E. hymenidermum* for a discussion of the differences among morphologically similar species.

***Entoloma discoloratum* Largent, sp. nov.**

PLATE 5

MYCOBANK MB804381

Differs from *Entoloma albomagnum* by its orangish pileus disc, appressed fibrillose stipe discoloring yellowish then brownish, broader lamellae, farinaceous odor without a soapy component, and sclerobasidia.

TYPE — Australia, New South Wales, Central Hunter District, Barrington Tops National Park, within 20 m of 32°14'25.2"S 151°43'29.8"E, 25 April 2010, DL Largent 9936 (holotype DAR).

ETYMOLOGY — Derived from the Latin *discoloratus* (= discolored) for the discoloration of the pileus and stipe.

PILEUS 64–80 mm broad, 11–18 mm high; not hygrophanous, not translucent-striate; broadly convex and broadly umbonate becoming irregularly uplifted with age; mostly glabrous but obscurely fibrillose in places particularly near the margin, dull, sticky to the touch; orange white to pale orange to light orange (5A3–4or 5A2–3) in the center, off-white elsewhere; margin decurved at first becoming plane and then uplifted, entire and rimose then quickly eroded; context white, 3–8 mm deep above the stipe, nearly non-existent at the margin. ODOR of mature basidiomata distinctly farinaceous, particularly after being crushed. TASTE strongly farinaceous. LAMELLAE 20–35 mm long, 7–15 mm deep; moderately broad to broad at first and when expanded and mature, mostly sinuate, in a few places broadly adnexed or adnate; at first crowded or close and then nearly subdistant; off-white (5A2–3); margin smooth and concolorous. STIPE 67–148 mm long, 10–21 mm broad at apex, 10–14 mm broad in the middle, 13–15 mm broad at base, tapered at the base or ventricose in the middle and then tapered; decidedly and deeply appressed fibrillose along the entire surface; off white, solid and stuffed; basal tomentum absent. BRUISING REACTIONS pileus stains or bruises greyish orange (5B4); stipe discoloring yellowish then brownish (5A2 to 5B3 or 5E-F4) when handled.

BASIDIOSPORES distinctly angular, isodiametric to subisodiametric in profile view, $6.7\text{--}8.3 \times 5.8\text{--}8.5 \mu\text{m}$ ($x = 7.5 \pm 0.48 \times 7.0 \pm 0.59 \mu\text{m}$; $E = 0.92\text{--}1.20$; $Q = 1.07 \pm 0.08$ (isodiametric); $n = 31/1$). BASIDIA cylindro-clavate, slender, $42.1\text{--}50.3 \times 7.6\text{--}10.3 \mu\text{m}$ ($x = 46.0 \pm 3.04 \times 8.9 \pm 0.89 \mu\text{m}$; $E = 4.43\text{--}6.09$; $Q = 5.2 \pm 0.61$; $n = 7/1$), full of large irregularly shaped globules; 2- or 4-sterigmate. SCLEROBASIDIA rare, aborted $51\text{--}53.9 \times 8.4\text{--}10.7 \mu\text{m}$, wall $1.7\text{--}2.3 \mu\text{m}$ thick ($n = 2/1$), filled with large globules. HYMENIAL CYSTIDIA absent. LAMELLAR TRAMAL HYPHAE subparallel, relatively long and broad, $63.2\text{--}199.7 \times 13.0\text{--}29.9 \mu\text{m}$ ($n = 7/1$). PILEIPELLIS $140 \mu\text{m}$ thick, an entangled ixocutis, particularly evident near the center of the pileus, hyphae just below the surface, $3.3\text{--}5.8 \mu\text{m}$ wide ($n = 4/1$). PILEOCYSTIDIA mostly prostrate, a few semi-erect, slender,

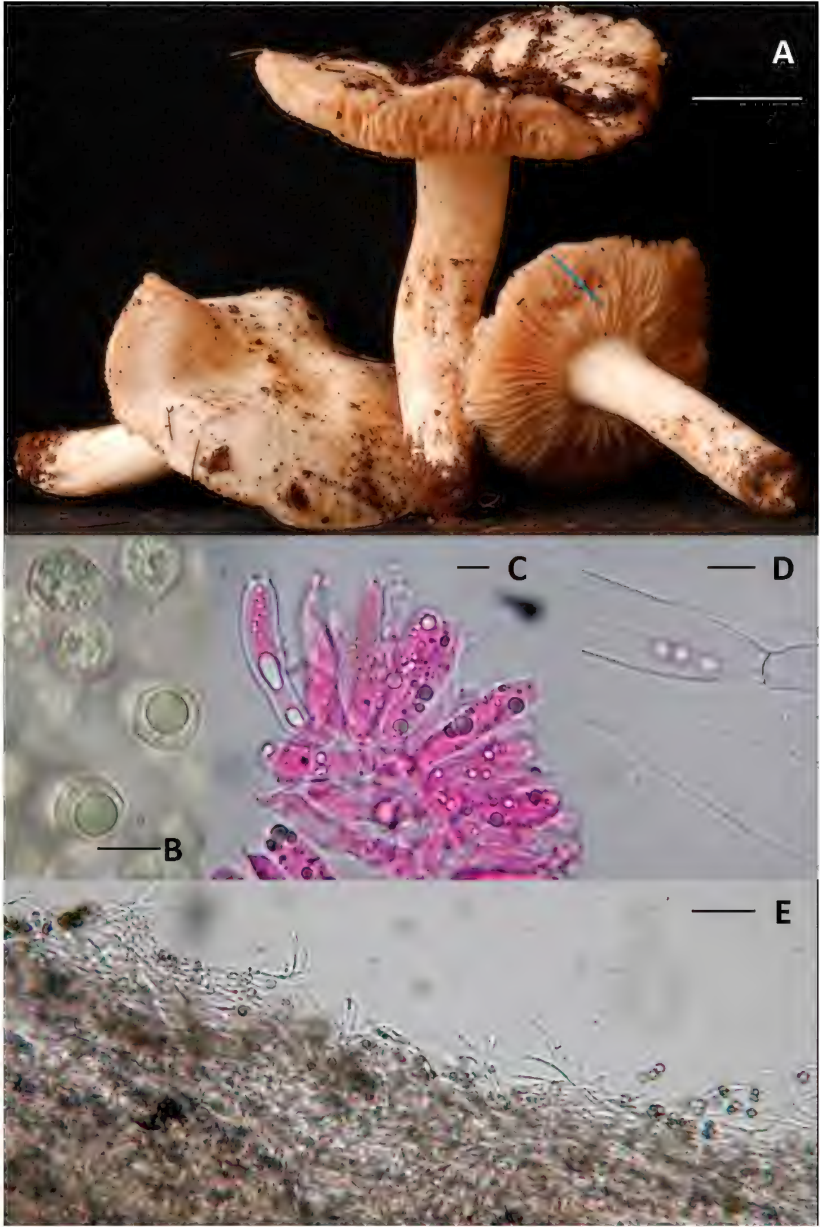


PLATE 5. *Entoloma discoloratum* (DLL 9936 holotype). A. Basidiomata. B. Basidiospores. C. Sclerobasidium on left; elsewhere thin-walled basidia and basidioles (1% phloxine stain). D. Hyphae of lamellar trama, large clamp on septum of top hyphae. E. Pileipellis, an ixocutis. Bars: A = 20 mm; B = 7 μ m; C = 10 μ m; D = 15 μ m; E = 35 μ m.

cylindric, $40.9\text{--}45.0 \times 2.0\text{--}3.0 \mu\text{m}$ ($n = 4/1$). PILEAL TRAMAL HYPHAE similar to the lamellar trama, $76.2\text{--}169.3 \times 16.9\text{--}35.3 \mu\text{m}$ ($n = 7/1$). STIPITIPPELLIS a cutis. CAULOCYSTIDIA and HYMENIAL CLUSTERS absent. OLEIFEROUS HYPHAE abundant in the lamellar trama, end cells may extend into the subhymenium. BRILLIANT GRANULES and LIPOID BODIES absent. PIGMENTATION non-existent. CLAMP CONNECTIONS abundant at the base of the basidia, on the hyphae of the lamellar trama and pileipellis.

ECOLOGY AND DISTRIBUTION - Scattered to gregarious and buried in the soil and leaf litter, forming a fairy ring around *Syncarpia glomulifera* and near *Allocasuarina torulosa* (Aiton) L.A.S. Johnson, New South Wales, Barrington Tops National Park, Jerusalem Creek Track, late April to early-mid May.

ADDITIONAL COLLECTIONS EXAMINED — AUSTRALIA. NEW SOUTH WALES, central Hunter District, Barrington Tops National Park, Jerusalem Creek Track. $32^{\circ}14'25.2''\text{S}$ $151^{\circ}43'29.8''\text{E}$, 10 May 2010, DL Largent 9970 (topotype DAR); $32^{\circ}14'23''\text{S}$ $151^{\circ}43'29''\text{E}$, 10 May 2011, DL Largent 10217.

DISTINCTIVE CHARACTERS — Large off-white, subviscid pileus with pale yellow orange colors in the center; strongly fibrillose stipe without fibrillose flocks that eventually bruises yellowish then brown, sclerobasidia, distinctly angular basidiospores, and an ixocutis-type pileipellis.

COMMENTS — *Entoloma discoloratum*, which clusters with *E. albomagnum* and *E. cretaceum*, can be classified in *Entoloma* sect. *Albida* Noordel. based on its white basidiomata (Noordeloos & Gates 2012).

Entoloma albomagnum is distinguished by its white pileus with faint yellow tinge at the center, silky fibrillose-scurfy white stipe that does not discolor, soapy odor when first collected, weakly angular basidiospores, lamellar and pileal trama composed of short barrel-shaped elements ($20\text{--}90 \times 4\text{--}15 \mu\text{m}$), and the absence of sclerobasidia (Noordeloos & Gates 2012). The similarly white *E. cretaceum* from Tasmania differs in its smaller chalky white basidiomata, the white watery fibrous stipe, and rancid-farinaceous odor (Gates & Noordeloos 2007, Noordeloos & Gates 2012).

***Entoloma kewarra* Largent, sp. nov.**

PLATE 6

MYCOBANK MB804382

Differs from *Entoloma praeluteum* by its subviscid pileus with a pruinose bloom at first, fibrillose stipe base, white context becoming greenish yellow, ixocutis, and the intracellular pigment in the pileipellis.

TYPE — Australia, Queensland, Cook region, Kewarra Beach coastal vine forest. Within 20 m of $16^{\circ}46'50.7''\text{S}$ $145^{\circ}41'24.8''\text{E}$, 12 March 2012, DL Largent 10275 (holotype BRI, isotype CNS).

ETYMOLOGY — referring to the type locality, Kewarra Beach coastal vine forest.

PILEUS 6–52 mm broad, 4–12 mm high; opaque, not hygrophanous, not translucent-striate; when immature conic-campanulate then convex, finally broadly convex to plane, at times broadly umbonate; at first entirely covered with a thin layer of yellowish white fibrils (2–3A–C7–8), with maturity the bloom showing spots when damaged or dry, eventually the surface becomes glabrous but sticky to the touch when bloom disappears; surface without bloom yellow (4A–B7) except light yellow (3 or 4A2–4) on the margin, when old and overly mature becoming entirely olive yellow (3C8); margin entire, at first incurved, when mature remaining incurved or becoming decurved; context yellowish white (3A3) becoming vivid yellow (2–3A7–8) above the stipe and slightly lighter (3A7) elsewhere, solid, and 2–6 mm thick above the stipe, 1 mm thick at the margin. ODOR farinaceous and somewhat pungent. TASTE bitter and farinaceous. LAMELLAE 2–17 mm long, 1–5 mm deep; in some narrowly adnate at first then adnexed, in most adnexed at all times, crowded then close, narrow at first then slightly more broad in some; when immature yellowish white to light yellow (4A2–3) becoming orange yellow (5A2) then light orange (4–5A4–5) with basidiospore production; margin smooth and concolorous. STIPE 25–100 mm long, 4–10 mm broad at the apex, in some flattened and 5×8 , 10×13 , or 13×15 mm broad at the apex, 5–15 mm broad in the middle, and 4–13 mm broad at the base, tapered; distinctly appressed-fibrillose; pale yellow to light yellow (2A2–3, 3A3, 4A4) becoming olive yellow (3C8) with age; context solid and stuffed then becoming hollow from the apex downward, white at first becoming greenish yellow on exposure and when cut becoming yellow (3A6–7) where hollow; basal tomentum absent. BRUISING REACTIONS stipe surface becoming pale yellow to light yellow (4A3–4) then olive or olive brown (3E–F2) where handled.

BASIDIOSPORES distinctly angular in larger basidiospores, indistinctly angular in smaller basidiospores, isodiametric to barely subisodiametric in all views, short hilar appendage, $5.3\text{--}6.8 \times 5.0\text{--}6.4 \mu\text{m}$ ($\bar{x} = 6.4 \pm 0.3 \times 6.0 \pm 0.3 \mu\text{m}$; $E = 1.00\text{--}1.19$; $Q = 1.07 \pm 0.05$ (isodiametric); $n = 32/1$). BASIDIA with abundant granules, narrowly clavate and hardly tapered, $25.7\text{--}37.5 \times 7.2\text{--}11.8 \mu\text{m}$ ($\bar{x} = 31.5 \pm 4.9 \times 8.9 \pm 1.2 \mu\text{m}$; $E = 2.74\text{--}4.94$; $Q = 3.61 \pm 0.71$; $n = 14/2$); 4-sterigmate, the sterigma short and up to $2 \mu\text{m}$ long. SCLEROBASIDIA absent. HYMENIAL CYSTIDIA absent. LAMELLAR TRAMAL HYPHAE subparallel, slightly narrow, $63.3\text{--}101.2 \times 5.4\text{--}9.7 \mu\text{m}$ ($\bar{x} = 76.0 \pm 11.6 \times 7.5 \pm 1.62 \mu\text{m}$; $E = 7.28\text{--}15.86$; $Q = 10.6 \pm 2.78$; $n = 10/1$). PILEIPELLIS an entangled ixocutis, $29.0\text{--}120.0 \mu\text{m}$ in depth. PILEOCYSTIDIA narrowly cylindro-clavate, at times with a slightly inflated and minutely rostrate apex, $13.9\text{--}29.5 \times 1.6\text{--}2.9 \mu\text{m}$ ($n/1 = 6$). PILEAL TRAMAL HYPHAE relatively short and narrow, $33.9\text{--}106.9 \times 3.7\text{--}14.9 \mu\text{m}$ ($\bar{x} = 55.8 \pm 24.0 \times 9.4 \pm 3.2 \mu\text{m}$; $E = 3.16\text{--}12.65$; $Q = 6.67 \pm 3.37$; $n = 12/1$). OLEIFEROUS HYPHAE and LIPOID GLOBULES absent. PIGMENTATION



PLATE 6. *Entoloma kewarra* (A-B DLL 10275 holotype; C-E DLL 10055). A. Basidiomata. B. Pileus surface with bloom of very finely appressed fibrils on pileal margin. C. Basidiospores. D. Basidium and basidioles (1% phloxine stain). E. Pileipellis, an ixocutis. Bar scale: A, B = 15; mm; Bars: C = 6 μ m; D = 9 μ m; E = 30 μ m.

intracellular and yellowish in the pileipellis, exudes a yellowish green exudate in 70% ethanol, water and 3% KOH. CLAMP CONNECTIONS present on all the tissues, narrow and small.

ECOLOGY AND DISTRIBUTION — Solitary to scattered in the open and in sand between a poorly defined heath community and coastal vine forest near a mangrove community in northern Queensland, Kewarra Beach, late January through late March.

ADDITIONAL COLLECTIONS EXAMINED — AUSTRALIA. QUEENSLAND, Cook Region, Kewarra Beach, 16°46'49.7"S 145°41'23.1"E, 28 January 2011, PN 50; 4 February 2011, PN 57; 16°49'00.3"S 145°43'49.3"E, 21 March 2011, DL Largent 10055; 16°46'50.8"S 145°41'24.6"E 18 March 2012, DL Largent 10289, PN 70; DL Largent 10290, PN 72.

DISTINCTIVE CHARACTERS — Basidiomata tricholomatoid and buried in the sandy substrate up to two-thirds the stipe length, pileus initially with a yellowish white pruinose bloom, subviscid pileus surface, stipe surface light or pale yellow becoming darker where handled, stipe context becoming greenish yellow with exposure, an ixocutis-type pileipellis, and narrowly clavate basidia.

COMMENTS — *Entoloma pamela*e and *E. kewarra* are strongly supported as sister taxa in our analyses. With its bright yellow colors and tricholomatoid basidiomata, *E. pamela*e (also from northeastern Queensland) differs in its shiny dry egg-shell smooth glabrous pileus, diffracted-scaly stipe base, white context turning yellow, narrower basidia, minutely externally encrusted pigmentation in the pileipellis, and cutis-type pileipellis. Additional *Entoloma* species with similar morphological features are discussed in the Comments section under *E. pamela*e.

***Entoloma pamela*e Largent, sp. nov.**

PLATE 7

MYCOBANK MB804383

Differs from *Entoloma praeluteum* by its smaller pileus and stipe, fibrillose-squamulose stipe base, longer basidia, mild and indistinct odor and taste, and narrow cheilocystidia.

TYPE — Australia, Queensland, Cook region, Danbulla National Park, Kauri Creek Track, within 20 m of 17°07'50.6"S 145°35'57.7"E, 28 February 2010, DL Largent 9753 (holotype BRI, isotype CNS).

ETYMOLOGY — in honor of Pamela Largent, the collector of the holotype.

PILEUS 11–40 mm broad, 5–15 mm high; opaque, not translucent-striate, hygrophanous; convex when young and not umbonate, upon expansion and maturity becoming broadly umbonate to faintly gibbous and either remaining convex or becoming broadly convex; shiny, moist, at all times decidedly glabrous and smooth like an egg-shell; at first yellow (3A6 or 7) when hygrophanous darker yellow (3B6 or 6–7, “mustard yellow” or “Nankeen yellow”); margin entire becoming broadly lobed, decurved; context (beneath a thick yellow rind) 5–7 mm deep above the stipe, <1 mm at the very margin,



PLATE 7. *Entoloma pamelae* (DLL9753 holotype) A. Basidiomata. B. Basidiospores. C. Basidia (1% phloxine stain). D. Cheilocystidia (1% phloxine stain). E. Pileipellis, a cutis. F. Pileocystidium with faint external incrustations (arrow). Bars: A = 20 mm; B, C = 5 μ m; D = 20 μ m; E = 15 μ m; F = 3 μ m.

yellow white (3A2) becoming brighter yellow (3A2–3) then pale yellow (3A3) upon exposure to air. ODOR and TASTE indistinct and mild. LAMELLAE 2–20 mm long, 0.5–4.0 mm deep, when young consistently narrow then moderately broad to sigmoid; at first adnexed with maturity remaining adnexed but at times becoming sinuate, crowded then close; yellowish at first becoming pinkish with basidiospore maturity and then distinctly contrasted when compared with the pileus and stipe colors; margin concolorous with the face, smooth, at times faintly denticulate. STIPE 32–60 mm long, 5–15 mm broad at apex, 4–8 mm broad at base; consistently narrowing to the base; at first faintly appressed-fibrillose becoming distinctly-appressed fibrillose with the fibrils matted and becoming $\pm$ fibrillose-squamulose towards base; pale yellow to pastel yellow then dull yellow (3 or 4A3–4), the darker colors more evident on handling; context at first hollow in the apical $\frac{1}{3}$ to $\frac{1}{4}$ and stuffed elsewhere, upon maturity becoming mostly hollow, white when first cut, quickly becoming yellow upon exposure to air; basal tomentum absent. BRUISING REACTIONS stipe bruises brownish on handling.

BASIDIOSPORES 5-angled in profile view, 4–5-angled in dorsiventral view, distinctly angular, small, isodiametric to heterodiametric, $5.0\text{--}7.6 \times 5.1\text{--}7.3 \mu\text{m}$ ($x = 6.4 \pm 0.53 \times 6.0 \pm 0.49 \mu\text{m}$ $E = 0.83\text{--}1.35$; $Q = 1.07 \pm 0.11$ [isodiametric]; $n = 30/1$). BASIDIA cylindric to cylindro-clavate and very narrow $33.7\text{--}38.7 \times 5.1\text{--}7.7 \mu\text{m}$ ($x = 35.6 \pm 1.8 \times 6.6 \pm 0.8 \mu\text{m}$; $E = 4.60\text{--}6.56$; $Q = 5.4 \pm 0.55$; $n = 9/1$); 4-sterigmate. SCLEROBASIDIA absent. HYMENIAL CYSTIDIA absent. CHEILOCYSTIDIA cylindric to narrowly obclavate, $24\text{--}37.7 \times 0.8\text{--}4.1 \mu\text{m}$ ($n = 6/1$), the ends of lamellar tramal hyphae protrude through the hymenium. LAMELLAR TRAMAL HYPHAE subparallel, very narrow, $55.1\text{--}113.1 \times 2.7\text{--}12.9 \mu\text{m}$ ($n = 6/1$). PILEIPELLIS a periclinally arranged cutis composed of narrow, cylindric hyphae, 10–30 μm deep and with an unknown material on the outer surface that stains golden yellow in 3% KOH; PILEOCYSTIDIA cylindric to narrowly cylindro-clavate, $24\text{--}40 \times 2.2\text{--}3.6 \mu\text{m}$. PILEAL TRAMAL HYPHAE not studied. STIPITPELLIS a cutis. CAULOCYSTIDIA and HYMENIAL CLUSTERS absent. OLEIFEROUS HYPHAE, BRILLIANT GRANULES, and LIPOID GLOBULES absent. PIGMENTATION minutely incrusting the outer walls of the pileipellis hyphae. CLAMP CONNECTIONS present at the base of the basidia, the cheilocystidia, and on the hyphae of the lamellar trama and pileipellis.

ECOLOGY AND DISTRIBUTION — Scattered to gregarious in leaf humus beneath an unidentified species of *Casuarina* or *Acacia* in a dry sclerophyll forest in northern Queensland, Danbulla National Park, Kauri Creek Track from mid-February to late March.

ADDITIONAL COLLECTIONS EXAMINED—AUSTRALIA. QUEENSLAND, Cook Region, Danbulla National Park, Kauri Creek Track, $17^{\circ}07'59.1''\text{S}$ $145^{\circ}35'55.6''\text{E}$, 2 March

2010, DL Largent 9763; 17°07'56.3"S 145°35'54.3"E 17 March 2010, DL Largent 9787; 17°08'02.4"S 145°35'51.7"E, 27 March 2012, DL Largent 10352.

DISTINCTIVE CHARACTERS — Basidiomata yellow in contrast to the pinkish mature lamella, narrow yellowish immature lamellae, pileus glabrous and smooth like the surface of an egg, pileal context pale yellow beneath a thick bright yellow rind, small ($x = 6.4 \times 6.0 \mu\text{m}$) distinctly angular basidiospores, cylindric to obclavate cheilocystidia, minutely encrusted pigment on the external pileipellis hyphal walls.

COMMENTS — *Entoloma praeluteum* Corner & E. Horak (from Malaysia) differs from *E. pamela* by the larger (40–80 mm broad) pileus, longer (50–80 mm) stipe, farinaceous odor, shorter (25–30 μm) basidia, and lack of cheilocystidia (Horak 1980).

Entoloma flavidum (Masse) Corner & E. Horak (from Singapore, Malaysia, and Kerala, India) and *E. xanthomyces* Corner & E. Horak (from Singapore) have somewhat similar basidiome colors and stature as *E. pamela* but differ in their broader (≥ 140 mm) pileus and white to pallid immature lamellae that become subdecurrent or decurrent with age. Additionally, in *E. flavidum* the basidiospores are larger (9–11 $\times$ 6.5–7.5 μm) and the basidia are longer (25–65 mm long) than those of *E. pamela* (Horak 1980; Manimohan et al. 1995, 2006).

***Entoloma rugosiviscosum* Largent sp. nov**

PLATES 8–9

MYCOBANK MB804384

Differs from *Entoloma conspicuum* by its smaller basidiomata, the radial rugose viscid pileus, brown stipe, and ixotrichodermium.

TYPE — Australia, Queensland, Cook region, Daintree National Park, Tribulation section, Marrjda Track, within 20 m of 16°08'18.5"S 145°26'26.0"E, 20 March 2009, DL Largent 9676 (**holotype** BRI, **isotype** CNS).

ETYMOLOGY — from the Latin adjectives *rugosus* + *viscosus* referring to rugose viscid pileus surface.

PILEUS 55–75 mm broad, 15 mm high; not hygrophanous, not striate, and not translucent; broadly convex and umbonate; shiny, viscid and sticky to the touch and remaining so 14 hours after collecting; scummy on the disc, radially-rugose elsewhere; medium dark yellow brown (5E-F5) on the disc and brownish orange to light brown (5C-D4–5) elsewhere, eventually entirely greyish orange with age and fading; margin greyish orange (5B2–3), decurved and even, elastic, and extends past lamellae up to 2 mm; context solid, brownish beneath the cuticle, white elsewhere, 10 mm broad above the stipe apex, 1–1.5 mm at the margin. **ODOR** mild to mildly pungent. **TASTE** mild. **LAMELLAE** 25–26 mm long, 11–13 mm deep; uncinat to adnexed, at times nearly free; white at first; subdistant, more or less ventricose and broad; margin smooth then eroded with age,



PLATE 8. *Entoloma rugosiviscosum* (DLL9676 holotype). A. Basidiome with rugose pileus. B. Lamellae with eroded margins and stipe apex. Bar = 10 mm.

concolorous. STIPE 50–51 mm long, 11–14 mm broad at the apex, 9.5–14 mm broad in the middle, 7–15 mm broad at the base, more or less clavate-tapered, white at first discoloring yellowish (3A2–3) with age and handling, minutely

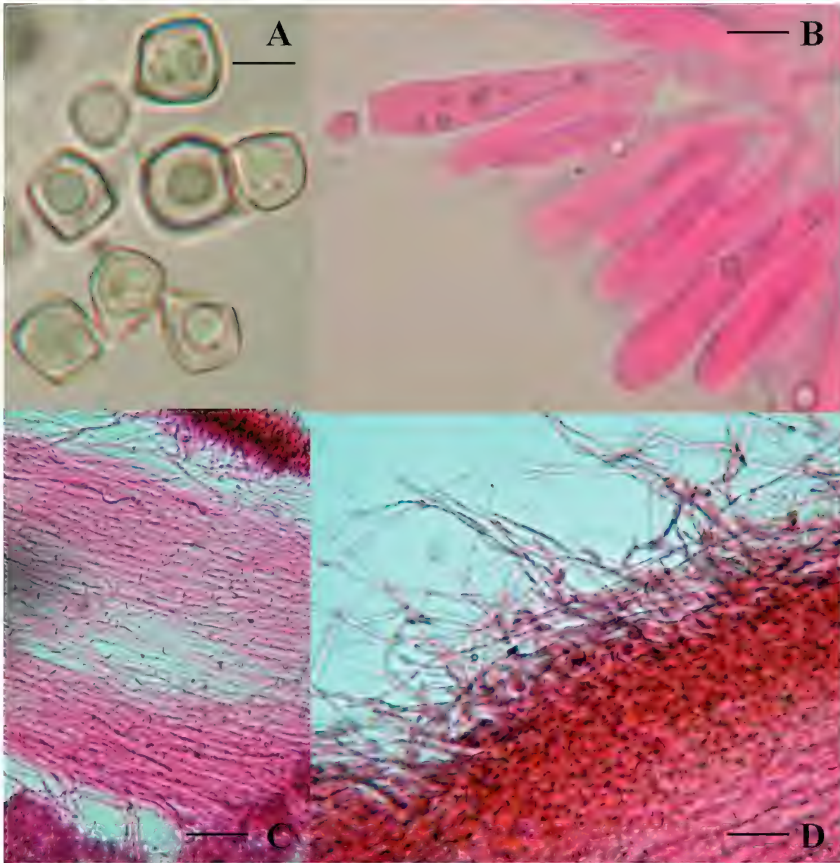


PLATE 9. *Entoloma rugosiviscosum* (A. DLL9676 holotype; B–D. DLL 9644, 1% phloxine stain). A. Basidiospores. B. Basidia, basidioles, clamp connection. C. Lamellar trama with gelatinized subhymenium, section slightly squashed. D. Pileipellis, an ixotrichodermium. Bars: A = 5 μ m; B = 8 μ m; C, D = 40 μ m.

appressed-fibrillose; flesh white, fibrous-stuffed then hollow in the center with age. BRUISING REACTIONS basidiomata discoloring yellowish with handling.

BASIDIOSPORES typically cuboidal and distinctly angular in all views, rarely 5-sided, small, $4.8\text{--}7.0 \times 4.1\text{--}6.6 \mu\text{m}$ ($x = 5.8 \pm 0.4 \times 5.4 \pm 0.5 \mu\text{m}$; Q $0.87\text{--}1.25$; E 1.07 ± 0.08 ; $n = 52/2$). BASIDIA 4-sterigmate, long and narrow, $33.1\text{--}44.7 \times 6.4\text{--}9.7 \mu\text{m}$ ($x = 38.1 \pm 3.4 \times 7.99 \pm 1.1 \mu\text{m}$; Q $3.76\text{--}6.23$; E 4.85 ± 0.8 ; $n = 10/1$). SCLEROBASIDIA absent. HYMENIAL CYSTIDIA absent. LAMELLAR TRAMA $318\text{--}400 \mu\text{m}$ wide; subhymenium gelatinized and broad, $40\text{--}56 \mu\text{m}$ wide. LAMELLAR TRAMAL HYPHAE subparallel to nearly parallel, short and broad, $38.5\text{--}102.2 \times 12.7\text{--}17.6 \mu\text{m}$. PILEIPELLIS an ixotrichodermium with cylindric hyphae $2\text{--}3$

µm diam., walls irregular and gelatinized. PILEAL TRAMAL HYPHAE subparallel, relatively short and broad, $61.2\text{--}133.5 \times 15.2\text{--}31.0$ µm. STIPITYPELLIS a cutis but with solitary but scattered basidia-like cells at the apex. STIPE TRAMAL HYPHAE nearly parallel, narrow in the outer portions, short and broad in central area and then $81.7\text{--}169.8 \times 15.2\text{--}36.9$ µm. OLEIFEROUS HYPHAE abundant in the trama of the pileus, lamellae, and stipe. BRILLIANT GRANULES and LIPOID GLOBULES absent. PIGMENTATION cytoplasmic, brownish and uniform in the hyphae of the pileipellis. CLAMP CONNECTIONS abundant and present in all tissues.

ECOLOGY & DISTRIBUTION — Solitary, humicolous, adjacent to the pavement on the Marrdja Track, 15–50 m from parking lot, Daintree National Park, Tribulation Section.

ADDITIONAL COLLECTIONS EXAMINED — AUSTRALIA. QUEENSLAND, Cook Region, Daintree National Park, Tribulation section, Marrdja Track, $16^{\circ}08'18.5''\text{S}$ $145^{\circ}26'26.0''\text{E}$, 12 March 2009, DL Largent 9644.

DISTINCTIVE CHARACTERS — Radially rugose viscid yellow brown pileus that fades to brownish orange or light brown, white stipe discoloring yellowish, basidiospores mostly cuboidal and small ($4.8\text{--}7.0 \times 4.1\text{--}6.6$ µm), an ixotrichodermium-type pileipellis, long narrow basidia.

COMMENTS — Phylogenetically *E. rugosiviscosum* clusters with several species including *E. prunuloides* (Fr.) Quél., *E. albomagnum*, and *E. cretaceum*. Excluding *E. ochreoprunuloides* Morgado & Noordel.), most of these species possess a tacky, sticky, subviscid, viscid, or glutinous pileus surface with an ixocutis- or ixotrichodermium-type pileipellis. *Entoloma conspicuum* E. Horak from Papua New Guinea resembles *E. rugosiviscosum* in its tricholomatoid basidiomata, brown rugose to subvenous pileus, and cuboidal basidiospores but differs by the cutis-type pileipellis and larger basidiomata (Horak 1976, 1980). *Entoloma rugosostriatum* Largent & T. W. Henkel from Guyana also has a brown rugose pileus and tricholomatoid stature but differs in its isodiametric nodulose basidiospores (Largent et al. 2008).

***Entoloma guttulatum* Largent, sp. nov.**

PLATES 10–11

MYCOBANK MB 807410

Differs from *Entoloma pingue* by the brown pileus, lamellae with discolored spots, larger basidia, and unusual pileipellis.

TYPE — Australia, Queensland, Cook region, Mossman National Park, 20 m from $16^{\circ}28'17.1''\text{S}$ $145^{\circ}19'51.2''\text{E}$, 18 March 2010, DL Largent 9791 (holotype BRI, isotype CNS).

ETYMOLOGY — from the Latin adjective *guttulatus* referring to droplets on the lamellar edge that dry as reddish brown spots

PILEUS 80–82 mm broad, 20 mm high; opaque, not hygrophanous, not translucent-striate; not umbonate, convex then uplifted; moist, glabrous to



PLATE 10. *Entoloma guttulatum* (DLL9791 holotype). A. Basidiome. B. Pileus surface. Bar = 13 mm.

the eye but under 4× to 20× subfelty or suede-like and with minute colorless pruinae; between greyish brown and yellowish brown (5D-E3–4) fading to between light orange and grayish orange (5A-B5–6) when old; margin plane then uplifted, wavy and crenulate. ODOR and TASTE unpleasant and slightly farinaceous. LAMELLAE 30–35 mm long, 9–10 mm deep, broad; adnate but a decurrent or subdecurrent tooth or subdecurrent; greyish orange (6B4) when mature; margin smooth and concolorous, with droplets as in some *Hebeloma* sp. that are abundant and dry as reddish brown spots. STIPE 60–100 mm long, 20 mm broad at the apex, 14 mm broad at base; longitudinally appressed fibrillose; grayish orange (6B4); context stuffed becoming hollow with age; basal tomentum absent. BRUISING REACTIONS stipe surface developing brownish orange to light brown (6C-D4) areas with age and handling.

BASIDIOSPORES distinctly angular, 5–6-angled, isodiametric to subisodiametric in profile view, isodiametric in polar view, $7.0\text{--}9.2 \times 6.7\text{--}8.8 \mu\text{m}$ ($x = 8.1 \pm 0.6 \times 7.8 \pm 0.5 \mu\text{m}$; $E = 0.9\text{--}1.3$, $Q = 1.04 \pm 0.08$ (isodiametric); $n = 60/2$). BASIDIA long and cylindro-clavate, $45.7\text{--}60.9 \times 7.4\text{--}11.2 \mu\text{m}$ ($x = 53.5 \pm 5.7 \times 9.6 \pm 1.3 \mu\text{m}$; $E = 4.79\text{--}6.16$, $Q = 5.64 \pm 0.56$; $n = 6/1$); 2- or 4-sterigmate. SCLEROBASIDIA absent. HYMENIAL CYSTIDIA absent. LAMELLAR TRAMAL HYPHAE $57.6\text{--}112.2 \times 8.8\text{--}13.6 \mu\text{m}$ ($n = 7/1$). PILEIPELLIS 48–70 μm deep, a colorless anticlinal layer of slender, entangled hyphae, 3–4 μm in diam, beneath which is a pigmented, densely entangled layer of hyphae; terminal cells cylindric to narrowly obclavate to rostrate-ventricose, $28.2\text{--}43.0 \times 3.2\text{--}5.3 \mu\text{m}$ ($n = 6/1$). PILEAL TRAMAL HYPHAE composed of broad cells. $34.9\text{--}59.9 \times 7.4\text{--}16.8 \mu\text{m}$ ($E = 2.54\text{--}6.13$; $n = 6/1$). STIPITIPELLIS a cutis. CAULOCYSTIDIA and HYMENIAL CLUSTERS absent. OLEIFEROUS HYPHAE, LIPOID GLOBULES and BRILLIANT GRANULES absent in the trama; basidia with abundant granules. PIGMENTATION colorless in the pileipellis, parietal in the entangled layer. CLAMP CONNECTIONS present in all tissues.

ECOLOGY & DISTRIBUTION — Solitary in leaf humus, Mossman and Daintree National Parks, far Northern Queensland, mid-March.

ADDITIONAL COLLECTIONS EXAMINED — AUSTRALIA. QUEENSLAND, Cook Region, Daintree National Park, Tribulation section, Emmagen Creek Track, $16^{\circ}02'19.7''\text{S}$ $145^{\circ}27'41.7''\text{E}$, 15 March 2010, DL Largent 9783.

DISTINCTIVE CHARACTERS — Tricholomatoid basidiomata, subfelty brown pileus, lamellae with droplets drying as reddish brown spots, unpleasant taste and odor, and a pileipellis as an anticlinal layer of entangled slender colorless hyphae with narrow 3–5 μm wide terminal cells.

COMMENTS — Phylogenetically *Entoloma guttulatum* clusters with *E. kewarra*, *E. pamela*, and *E. illinitum* (from Guyana) but few morphological features

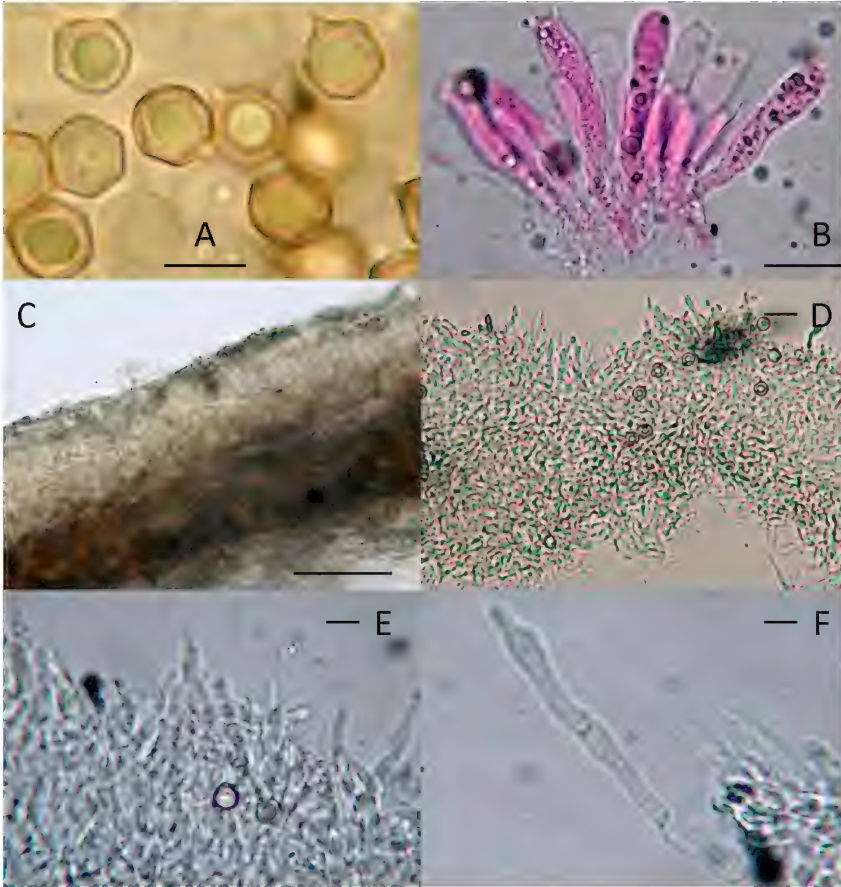


PLATE 11. *Entoloma guttulatum* (DLL9791 holotype). A. Basidiospores. B. Basidia, basidioles. C. Pileipellis (radial section at pileus disc). D. Pileipellis (squash mount) E. Pileipellis (squash mount) F. Pileocystidium. Bars: A = 8 μm ; B = 20 μm ; C = 25 μm ; D = 35 μm ; E = 10 μm ; F = 5 μm .

are shared between species. For example, the basidiospores are very small and distinctly angular in *E. kewarra* and *E. pamelae*, small and obscurely angular in *E. illinitum*, and large and distinctly angular in *E. guttulatum*.

Entoloma pingue Corner & E. Horak (from a *Casuarina* forest in the Solomon Islands), which shares a large fleshy stature, decurrent lamellae, and isodiametric basidiospores (7–9 μm diam.) with *E. guttulatum*, can be distinguished by its pale fuscous pileus, stipe changing to pale brown, white lamellae without reddish spots, 30–40 μm long basidia, and pigmented pileipellis (Horak 1980).

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Literature cited

- Aime MC, Largent DL, Henkel TW, Baroni TJ. 2010. The *Entolomataceae* of the Pakaraima Mountains of Guyana IV: new species of *Calliderma*, *Paraecilia* and *Trichopilus*. *Mycologia* 102: 633–649. <http://dx.doi.org/10.3852/09-162>
- Baroni TJ, Matheny PD. 2011. A re-evaluation of gasteroid and cyphelloid species of *Entolomataceae* from Eastern North America. *Harvard Papers in Botany* 16: 293–310. <http://dx.doi.org/10.3100/0.25.016.0205>
- Baroni TJ, Hofstetter V, Largent DL, Vilgalys R. 2011. *Entocybe* is proposed as a new genus in the *Entolomataceae* (*Agaricomycetes*, *Basidiomycota*) based on morphological and molecular evidence. *North American Fungi* 6: 1–19. <http://dx.doi.org/10.2509/naf2011.006.012>
- Bergemann SE, Largent DL, Abell-Davis SE. 2013. *Entocybe haastii* from Watagans National Park, New South Wales, Australia. *Mycotaxon* 126: 61–70. <http://dx.doi.org/10.5248/126.61>
- Co-David D, Langeveld D, Noordeloos ME. 2009. Molecular phylogeny and spore evolution of *Entolomataceae*. *Persoonia* 23: 147–176. <http://dx.doi.org/10.3767/003158509X480944>
- Eyssartier G, Randrianjohany E, Buyck B. 2012. Trois entolomes (*Entolomatales*, *Basidiomycota*) à épicutis hyméniforme de la réserve spéciale d'Ambohijantely, Madagascar. *Cryptogamie Mycologie* 33(2): 157–166. <http://dx.doi.org/10.7872/crym.v33.iss2.2012.157>
- Gates GM, Noordeloos ME. 2007. Preliminary studies in the genus *Entoloma* in Tasmania I. *Persoonia* 19: 157–226.
- Horak E. 1976. On cuboid-spored species of *Entoloma* (*Agaricales*). *Sydowia* 28: 171–236.
- Horak E. 1980. *Entoloma* (*Agaricales*) in Indomalaya and Australasia. *Beihefte zur Nova Hedwigia* 65: 1–352.
- Karstedt F, Capelari M. 2010. New species and new combinations of *Calliderma* (*Entolomataceae*, *Agaricales*). *Mycologia*, 102: 163–173. <http://dx.doi.org/10.3852/09-019>
- Katoh K, Standley DM. 2013. MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution*: 30: 772–780. <http://dx.doi.org/10.1093/molbev/mst010>
- Kornerup A, Wanscher JH. 1978. *Methuen handbook of colour* 3rd ed. Richard Clay Ltd: Chichester, Sussex.
- Largent DL. 1986. *How to Identify Mushrooms to Genus I*. Mad River Press Inc: Eureka, California.
- Largent DL. 1994. *Entolomatoid fungi of the western United States and Alaska*. Mad River Press Inc: Eureka, California.

- Largent DL, Abell-Davis SE. 2011. Observations on *Inocephalus virescens* comb. nov. and *Alboleptonia stylophora* from northeastern Queensland. *Mycotaxon* 116: 231–245. <http://dx.doi.org/10.5248/116.231>
- Largent DL, Henkel TW, Aime MC, Baroni TJ. 2008. The *Entolomataceae* of the Pakaraima Mountains of Guyana I: four new species of *Entoloma* s. str. *Mycologia* 100: 132–140. <http://dx.doi.org/10.3852/mycologia.100.1.132>
- Largent DL, Abell-Davis SE, Cummings GA, Ryan KL, Bergemann SE. 2011a. Saxicolous species of *Claudopus* (*Agaricales*, *Entolomataceae*) from Australia. *Mycotaxon* 116: 253–264. <http://dx.doi.org/10.5248/116.253>
- Largent DL, Bergemann SE, Cummings GA, Ryan KL, Abell-Davis SE, Moore S. 2011b. *Pouzarella* (*Agaricales*, *Entolomataceae*) from New South Wales (Barrington Tops National Park) and northeastern Queensland. *Mycotaxon* 117: 435–483. <http://dx.doi.org/10.5248/117.435>
- Largent DL, Bergemann SE, Abell-Davis SE, Kluting KL, Cummings GA. 2013a. Three new *Inocephalus* species with cuboid basidiospores from New South Wales and Queensland, Australia. *Mycotaxon* 123: 301–309. <http://dx.doi.org/10.5248/123.301>
- Largent DL, Bergemann SE, Abell-Davis SE, Kluting KL, Cummings GA. 2013b. Five *Leptonia* species from central New South Wales and Queensland, Australia. *Mycotaxon* 125: 11– 35. <http://dx.doi.org/10.5248/125.11>
- Liu YJ, Whelen S, Hall BD. 1999. Phylogenetic relationships among *Ascomycetes*: evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* 16: 1799–1808.
- Manimohan P, Joseph AV, Leelavathy KM. 1995. The genus *Entoloma* in Kerala State, India. *Mycological Research* 99: 1083–1097. [http://dx.doi.org/10.1016/S0953-7562\(09\)80777-6](http://dx.doi.org/10.1016/S0953-7562(09)80777-6)
- Manimohan P, Noordeloos ME, Dhanya AM. 2006. Studies in the genus *Entoloma* (*Basidiomycetes*, *Agaricales*) in Kerala State, India. *Persoonia* 19(1): 45–93.
- Matheny PB. 2005. Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; *Agaricales*). *Molecular Phylogenetics and Evolution* 35: 1–20. <http://dx.doi.org/10.1016/j.ympev.2004.11.014>
- Morgado LN, Noordeloos ME, Lamoureux Y, Geml J. 2013. Multi-gene phylogenetic analyses reveal species limits, phylogeographic patterns, and evolutionary histories of key morphological traits in *Entoloma* (*Agaricales*, *Basidiomycota*). *Persoonia* 31: 159–178. <http://dx.doi.org/10.3767/003158513X673521>
- Noordeloos ME. 1992. *Entoloma* s.l. in *Fungi Europaei* vol. 5. Ed. Candusso: Alassio, Italy.
- Noordeloos ME. 2005. *Entoloma* s.l. in *Fungi Europaei* vol. 5a. Ed. Candusso: Alassio, Italy.
- Noordeloos ME, Gates GM. 2012. The *Entolomataceae* of Tasmania. *Fungal Diversity Research Series* 22: 1–399. <http://dx.doi.org/10.1007/978-94-007-4679-4>
- Orton PD. 1991. A revised list of the British Species of *Entoloma* sensu lato. *The Mycologist* 5: 123–138.
- Romagnesi H. 1956. Les Rhodophylles du Congo Belge d'après les récoltes de Mme Goossens-Fontana. *Bulletin du Jardin Botanique de l'État à Bruxelles* 26: 137–182.
- Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690. <http://dx.doi.org/10.1093/bioinformatics/btl446>
- Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for RAxML web servers. *Systematic Biology* 57: 758–771. <http://dx.doi.org/10.1080/10635150802429642>
- Thiers B. 2012. Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/> [accessed May 2012].